Restoration Ecology
THE JOURNAL OF THE SOCIETY FOR ECOLOGICAL RESTORATION INTERNATIONAL

RESEARCH ARTICLE

Effects of Prescribed Burning and Mechanical Bush Clearing on Ungulate Space Use in an African Savannah

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Abstract

Savannah ecosystems exhibit constant transitions between states dominated by trees and states dominated by a combination of trees and grasses. Transitions between these states are driven by interactions between fire and herbivory. Bush encroachment (i.e. an increase in the density of woody vegetation) is often caused by anthropogenic disturbance such as climate change, invasive plants, fire control, and livestock practices. As bush encroachment alters the dynamics between fire and herbivory, it may have significant impact on savannah ecosystems. Two of the most common measures to mitigate bush encroachment are prescribed burning and bush clearing by mechanical treatments. We studied the effects of these two mitigation measures on ungulate space use in Lapalala Wilderness, a private conservation area within the Waterberg Biosphere Reserve, northern South Africa. Burning and bush clearing affected both the overall abundance and the species composition of ungulates at particular patches, but these effects were influenced by habitat and the type of bush clearing treatment. Contrary to our expectations, most species occurred less frequently in burnt patches, and also less frequently in patches that had been bush cleared. Our results suggest that combined effects of fire and bush clearing may have positive effects on grazers and negative effects on browsers. Although our sampling design did not allow us to fully resolve interactive effects of burning and bush clearing treatments across habitats, our study highlights the fact that there are complex ecological consequences of habitat alterations in savannah ecosystems.

Key words: antelope, habitat management, herbivore, herbivory, savannah ecology.

Introduction

African savannah ecosystems are home to a large number of mammalian herbivores and support high species richness across several trophic levels (Klop & van Goethem 2008). Savannah ecosystems are dynamic and exhibit constant transitions between states dominated by trees and more open states dominated by a combination of trees and grasses (Low & Rebelo 1996; Van Langevelde et al. 2003; Wiegand et al. 2006). These transitions are typically driven by interactions between fire and herbivory (Sheuyange et al. 2005; Klop & Prins 2008; Staver et al. 2009). Tree dominated states are promoted by increased grazing pressure which results in increased woody vegetation due to the reduced fuel load which prevents frequent and intense fires. Transitions into tree and grass dominated states occur when browsers suppress woody biomass, which results in an increased fuel load through stimulated grass growth and subsequently more intense fires reducing woody biomass even further (Low & Rebelo 1996; Scholes & Archer 1997; Van Langevelde et al. 2003; Sawadogo et al. 2005; Sheuyange et al. 2005; Wiegand et al. 2006; Staver et al. 2009). Because of this dynamic regulation of savannah systems, manipulative habitat alterations are common practice in many African conservation areas to direct animal movement and habitat use, and to limit the severity of very high intensity fires caused by fuel accumulation (Anderson & Müller 2000; Smit 2004; Archibald et al. 2005; Klop et al. 2007; Long et al. 2008).

Bush encroachment is an increase in the density, cover and biomass of woody plant species, which is becoming increasingly common in arid and semiarid environments. In this study, we use the term woody vegetation and bush to denote woody plant species, but we recognize that the term shrub has been equally used in the literature. Reviews highlight that bush encroachment has mixed effects on ecosystem structure and functioning (Van Auken 2000, 2009; Eldridge et al. 2011), including that shrub traits influence the functional outcome of encroachment. Bush encroachment in savannah habitat also alters the dynamic processes between fire and herbivory (Strang 1973; Tainton 1999; Smit 2004; Wiegand et al. 2006). Bush encroachment can either be caused by an

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doi: 10.1111/j.1526-100X.2012.00877.x

increase in the biomass of already established plants, or an increase in tree density owing to the establishment of seedlings (Strang 1973; Tainton 1999; Smit 2004). There are many factors that trigger bush encroachment, either singularly or in combinations. These include heavy grazing pressure, absence of fires, absence of mega-herbivores such as elephants that damage trees, increases in CO_2 and N deposition (Archer 2010), reduced fire frequency (Scholes & Archer 1997), increased atmospheric carbon dioxide due to long-term climate change (Knapp et al. 2008), invasive aliens (Archer 2010), and potentially, predator suppression (Kerley & Whitford 2009).

In African savannahs, prescribed burning is frequently used to limit the impact of bush encroachment and restore areas to improve the quantity and quality of forage for grazing herbivores (Archibald et al. 2005; Sheuyange et al. 2005; Klop and Prins 2008; Staver et al. 2009). However, because of increased grazing intensity in burnt areas, woody vegetation often accumulates successively after fire so that the effects of burns on bush encroachment may be limited (Sheuyange et al. 2005; Staver et al. 2009). Such limiting effects by increased grazing pressure can, on the other hand, be counteracted by browsing which suppresses woody vegetation and hence promotes the maintenance of open grasslands. This suggests that both browsers and frequent fire are needed to suppress the development of dense woody cover (Hassan et al. 2007; Staver et al. 2009), although the effects are short term irrespective of browsing pressure when encroachment is at an advanced stage (Trollope 1982; Sheuyange et al. 2005). Moreover, because grass is the primary fuel for fires in savannah habitat, suppression of grasses due to bush encroachment often leads to insufficiently intense fires to control woody vegetation (Trollope 1982; Van Langevelde et al. 2003; Sawadogo et al. 2005). Therefore, prescribed burning is often adapted in conjunction with treatments to mechanically remove woody plants to enable a sufficient amount of grass to accumulate as fuel. Mechanical methods employed to remove most of the woody layer, typically shredding or roller chopping, are often supplemented by chemical treatments on the cut stumps to reduce re-growth (Smit 2005).

The modifications of the savannah structure following burning and tree thinning will have significant effects on the spatial distribution of available food for both grazers and browsers (Anderson & Müller 2000; Long et al. 2008). Both methods of ecosystem manipulation are therefore predicted to influence movement and habitat use by herbivores (Archibald et al. 2005). However, because of species-specific foraging preferences, effects may differ among herbivore species. In African savannahs, dense woodland habitats are preferred by obligate browsers such as greater kudu *Tragelaphus strepsiceros* and giraffe *Giraffa camelopardalis,* while mixed foragers such as impala *Aepyceros melampus* favor open woodland and grazers such as Burchell's zebra *Equus burchelli* and blue wildebeest *Connochaetes taurinus* prefer open grassland habitats (Ben-Shahar 1992). These altering habitat preferences among herbivore species, coupled with the importance of herbivory for savannah ecosystem functioning, makes it imperative to fully understand the ecological consequences of fuel reduction within savannah habitats (Long et al. 2008).

In this study we examined the effects of prescribed burning and mechanical bush clearing on habitat use by African ungulates in a mountain savannah region in South Africa. The dominant ungulates in our study area were blue wildebeest, giraffe, impala, kudu, and Burchell's zebra. We investigated the effects of fire and mechanical bush clearing on ungulate species composition in three habitat types, and tested the following specific predictions: (1) fire will increase the occurrence of both grazing and browsing species, (2) grazers will be attracted to areas that have been both cleared and burned, while browsers will prefer uncleared burnt plots, (3) bush clearing will increase the abundance of grazing species but decrease the abundance of browsing species.

Methods

Study Area

We conducted the study in Lapalala Wilderness, a privately owned game reserve in the Waterberg Biosphere Reserve in the Limpopo province, South Africa (23°51′S, 28°16′E; Fig. 1). The reserve is currently not open to the public, although occasional guided hunting parties are allowed on the property. The reserve is fenced, covers an area of approximately 36,000 ha and has a topography consisting of elevated plateaus and undulating rocky hills. It lies within a summer rainfall area with annual rainfall ranging from 650 to 900 mm (Low & Rebelo 1996). Average maximum summer temperature is 32°C and the average minimum summer temperature is 18°C. Average maximum winter temperature is 22°C and the average minimum winter temperature is 4°C, with frost commonly occurring (Ben-Shahar 1987).

The area is characterized by acidic soils which are derived from sandstone, quartz, and shale. The vegetation is classified as Waterberg moist mountain bushveld, which is characterized by the abundance of woody plant species such as *Terminalia sericea*, *Burkea africana*, and *Combretum* spp. (Low & Rebelo 1996). Grasses typically become lignified and unpalatable to herbivores near the beginning of the rainy season (Ben-Shahar 1987). Grazing and fire interactions are important determinants of plant community structure, while aspect also plays a key role in the distribution of plant species (Low & Rebelo 1996).

The Reserve has three main habitat types, which are based on three substrate types: red soils, sands, and quartzites (Fig. 1). Red soils have relatively high clay contents and are deep and base-rich. Indicator species of the vegetation found on red soils include woody *Dichrostachys cinerea,* a number of *Acacia* species, and the grass *Aristida congesta*. These areas are usually heavily encroached by sickle bush (*D. cinerea*), but are favored by wildlife due to high net productivity. Sand soils are characterized by the woody species *B. africana* and *T. sericea*. A large proportion of the land is covered by grasses such as *Eragrostis gummiflua* and *Panicum maximum*. Quartzite soils typically occur in the upland areas, and are characterized by semi-open arid

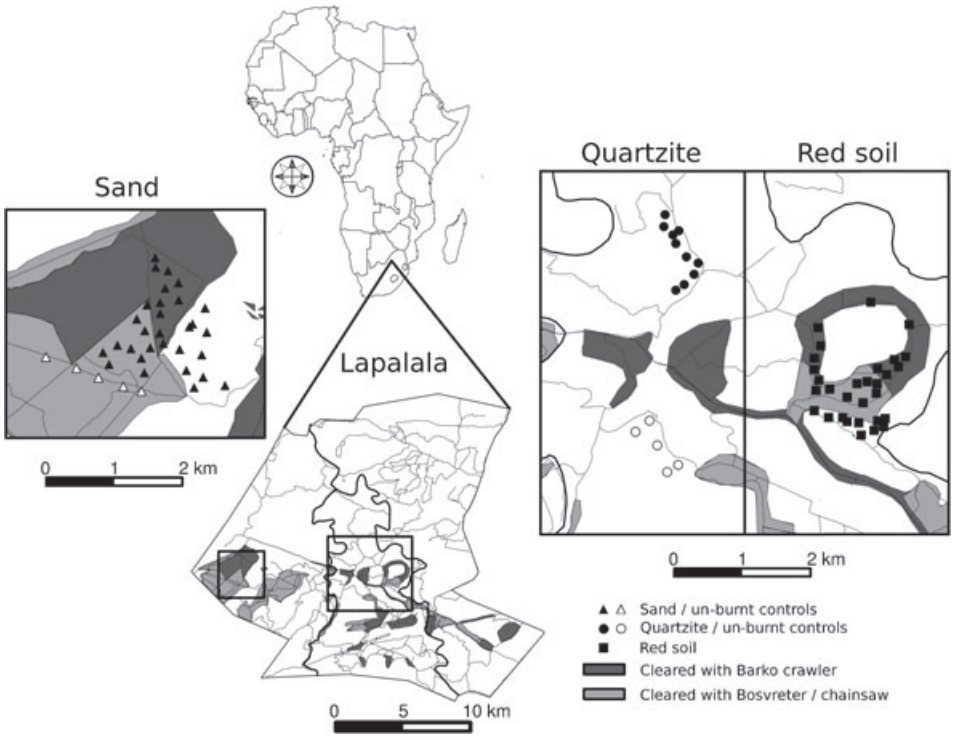

Figure 1. Map of Lapalala Wilderness including areas that had undergone different methods of bush clearing as well as locations of the sampled plot lines.

savannah characterized by the woody species *Diplorhynchus condylocarpon* and *Combretum apiculatum* and the grass *P. maximum* (Rutherford et al. 2006).

Lapalala Wilderness contains 22 herbivorous large mammal species, with the most numerous being Burchell's zebra and impala, followed by kudu and blue wildebeest. Large predators resident in the area are black-backed jackal *Canis mesomelas*, brown hyena *Hyaena brunnea*, leopard *Panthera pardus*, and crocodile *Crocodilus niloticus*.

A significant portion of Lapalala Wilderness is burned annually, depending on the rainfall received. The reserve is divided into burning blocks bounded by natural or artificial fire-breaks, and these blocks are burned on a rotational basis. These blocks are defined using roads, tracks, cleared fence-lines, rivers and water courses. For mechanical bush clearing in this study, Lapalala Wilderness used two primary methods; clearing with a barko crawler (http://www.barko.com) and manual clearing using a bosvreter (http://www.bosvreter.co.za/bosvreter.asp) or chainsaws (collectively called "bosvreter" throughout the article). While clearing with barko crawlers is highly unselective, clearing using bosvreters or chainsaws provides a more selective control of bush encroachment. For areas cleared with this latter approach, cut stumps of woody vegetation were immediately treated with the arboricide triclopyr.

Field Experimental Design

We distributed line transects evenly in the three habitat types described above (i.e. red soil, sand, and quartzite). Transects were spaced at least 100 m apart and transects were not allowed to cross. Along each transect, we placed 10 plots spaced 10 m apart and counted all ungulate pellets occurring within a radius of 2 m from the center of each plot, giving a plot size of 12.5 m^2. To relocate the plots, we permanently marked plots using iron reinforcement bars.

For red soil and sand habitat, we placed 10 transects each in uncleared areas, areas that had been cleared using a barko, and areas that had been cleared using a bosvreter (Table 1). As no bush clearing had occurred in quartzite habitat, we only investigated uncleared areas in this habitat. All areas except for the red soil habitat, which did not get burned for logistical reasons, were burned between June–November 2009 as part of the normal burn regime within the reserve. We sampled all transects prior to being burned in April and May 2009 and resampled all burnt transects again in June 2010, 8–10 months post burn. To enable us to control for temporal variation in pellet counts between the two sample periods that were not caused by burning, we also placed five transects in each of the two burnt habitats and sampled these in parallel with burnt transects (Table 1). The unburnt controls were placed in bosvreter cleared areas in the sand habitat (no uncleared areas were left unburnt adjacent to the burnt areas in this habitat) and in uncleared areas in the quartzite habitat.

We acknowledge that because our study only included one reserve, the design is pseudoreplicated on a landscape scale. The study does therefore not allow generalizations about the

Table 1. Number of sampled transects (each transect consisting of 10 plots spaced 10 m apart) in three habitats in Lapalala Wilderness.

	Uncleared		*Barko*		*Bosvreter*	
	Control	*Burnt*	*Control*	*Burnt*	*Control*	*Burnt*
Red soil[a]	10[b]		10[b]		10[b]	
Sand		10[b,c,d]		10[b,c]	5[e]	10[b,c,e]
Quartzite	5[e]	10[d,e]				

Plots were placed in uncleared patches, patches cleared using a barko crawler, and patches cleared using a bosvreter and chainsaw and in areas that were not burnt between the two sample periods (control transects) as well as areas that were burnt between the two sample periods (burnt patches).

[a] Red-soil transects were only sampled during the pre-burn sample period.

[b] Transects used in the model evaluating the effects of bush clearing in different habitats.

[c] Transects used in the model evaluating the effects of burning and bush clearing.

[d] Transects used in the model evaluating the effects of burning in different habitats.

[e] Transects used in the model evaluating the effects of burning on variation between the pre- and post-burn sample periods.

effects of bush treatments in savannah habitat. However, this single reserve represents a valuable opportunity to gain information about the effects of bush removal treatments on habitat use by ungulates.

Data Analyses

Because of difficulties in identifying individual pellet groups, we treated pellet data as binary presence/absence data for each species within each plot. We used mixed generalized linear models with a binomial error structure and a logit link function to evaluate the effects of burning and bush clearing in the three habitat types on the probabilities of finding ungulate pellets. Because of the incomplete sampling design, we created subset models to test specific hypotheses related to burn and bush clearing treatments. Although such an approach may differ from the general approach toward statistical modeling in ecology, it has recently been advocated as a more flexible alternative that may more fruitfully address biological questions (Hector et al. 2010).

To evaluate the effect of burning on variation in ungulate abundance between the two sample periods (i.e. pre- or post-burn), we constructed a model including transects from quartzite and sand habitats and with bush clearing treatment containing relevant controls (i.e. uncleared patches in quartzite habitat and bosvreter cleared patches in sand habitat; Table 1). In this model, we added sample period (pre- or post-burn), burn class (burnt or unburnt), habitat, and ungulate species as fixed terms. To evaluate the effects of burning in different habitats, we constructed a model including transects in burnt, uncleared areas in sand and quartzite habitats (Table 1). The model had the same fixed effect structure as described above with the exception of the exclusion of burn class. To evaluate the combined effects of burn and bush clearing, we constructed a model only including transects from the sand habitat. In this model, we used bush clearing treatment (uncleared, barko, and bosvreter), sample period (pre- or post-burn) and ungulate species as fixed effects. Finally, to evaluate the effects of bush clearing treatments in different habitats, we constructed a model containing transects from the sand and red soil habitats, but only from the pre-burn sampling (Table 1). In this model, we used habitat, bush clearing treatment and ungulate species as fixed effects.

In all models, we first added all possible interaction terms and sequentially tested models containing each fixed term against models including all other terms of the same interaction level (analogously to type II sums of square tests, e.g. Hector et al. 2010) using likelihood ratio tests (Crawley 2007). In all models, we added plot nested within transect nested within habitat as random effect structure. All analyses were carried out using the lme4 library for the statistical package R for Linux (http://www.r-project.org).

Results

The difference between quartzite and sand habitats with regards to variation in the probability of finding ungulate pellets between pre- and post-sampling was significantly influenced by whether plots had been burnt or not: ($\chi^2 = 9.59$, $df = 1$, $p < 0.01$). This result indicates that burning per se influenced differences in ungulate distribution between the two sample periods.

Contradictory to our first prediction, pellets from most ungulate species were found less frequently during the post-burn sampling. In uncleared patches, the most drastic declines were found for impala, kudu, and zebra in the quartzite habitat and for kudu and zebra in the sand habitat (Fig. 2A). In uncleared patches, habitat influenced how burning affected the overall probability of finding ungulate pellets pre- and post-burn ($\chi^2 = 4.46$, $df = 1$, $p = 0.03$), and the ungulate species composition also differed between pre- and post-burn sampling ($\chi^2 = 28.8$, $df = 5$, $p < 0.01$), although this effect on species composition did not significantly differ between quartzite and sand habitats ($\chi^2 = 5.11$, $df = 5$, $p = 0.40$). Within the sand habitat, bush clearing treatment influenced the difference in overall probability of finding ungulate pellets pre- and post-burn ($\chi^2 = 6.43$, $df = 2$, $p = 0.04$), but did not influence any differences in ungulate species composition pre- and post-burn ($\chi^2 = 15.4$, $df = 10$, $p = 0.12$; Fig. 2b). In accordance with our second prediction, the two grazers (blue wildebeest and zebra) increased more post burn in bush cleared areas compared to uncleared areas, but there were less consistent results for impala, kudu, and giraffe, all mixed foragers or browsers (Fig. 2b).

Bush clearing method significantly altered ungulate species composition ($\chi^2 = 25.9$, $df = 10$, $p < 0.01$), but these effects did not significantly differ between sand and red soil habitats ($\chi^2 = 12.4$, $df = 10$, $p = 0.26$). All species except impala in the red soil habitat appeared in fewer plots in the cleared patches compared to the uncleared controls, but there was great variation in the effect of the two bush clearing methods on individual species occurrences (Fig. 3). However, contrary to our last prediction, the two grazers, blue wildebeest and zebra, did not occur more frequently in cleared compared to uncleared patches.

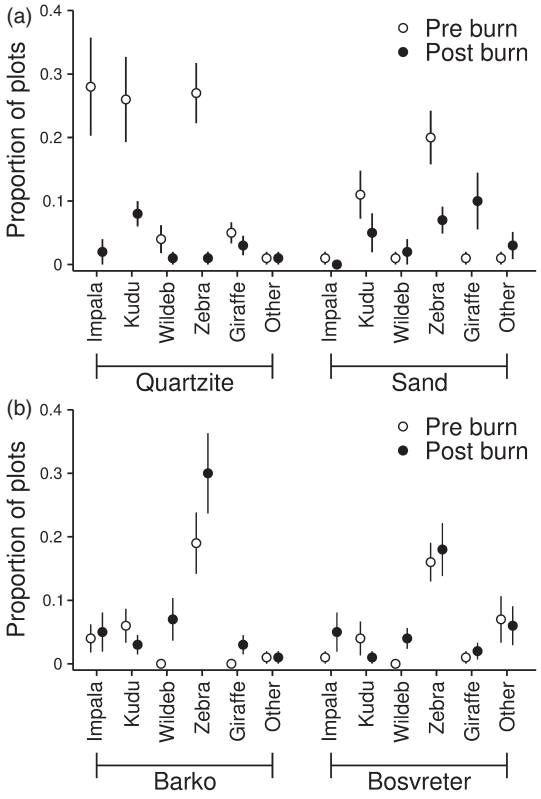

Figure 2. Proportion of plots (mean ± SE) with pellets of different ungulate species along transects sampled pre- and post-burn in uncleared patches in quartzite and sand habitat (a) and in patches in sand habitat that had been cleared with a barko crawler and manually using a bosvreter and chainsaw (b).

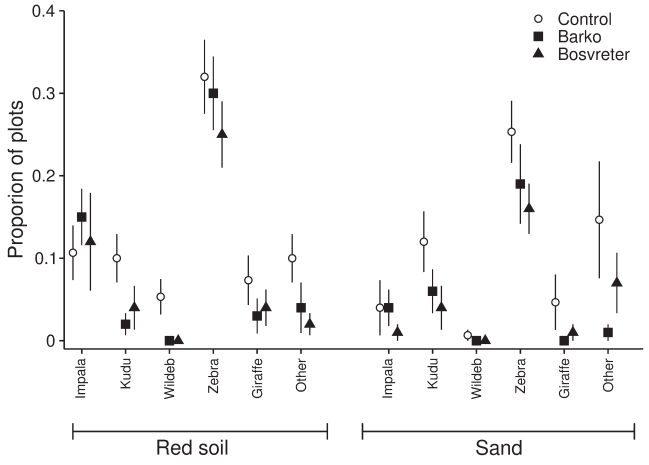

Figure 3. Proportion of plots (mean ± SE) with pellets from different herbivore species along transects placed in two different habitats and in patches that had undergone two different types of bush clearing as well as uncleared controls. All data are from pre-burn sampling.

Discussion

The investigated options for restoring vegetation structure following bush encroachment provide contrasting alterations to wildlife habitats. Fire is a broad scale disturbance that alters the structure as well as the taxonomic and chemical composition of plant communities in terrestrial ecosystems. Bush clearing, on the other hand, primarily modifies wildlife habitat by altering its vegetation structure. Moreover, our study included two separate bush clearing treatments, one unselective (Barko) and one selective (Bosvreter and chainsaw) in terms of which individual plants are disturbed or removed.

Prescribed burning and mechanic removal of woody vegetation both influenced the occurrences of ungulates. However, the effect of burning on ungulate space use was not uniform across habitats and our results contradict our first prediction (i.e. fire would uniformly increase ungulate abundance). Instead, with the exception of giraffe in quartzite habitats, we found lower occurrence of pellets from all ungulate species during the post-burn count. These results are consistent with Legge et al. (2008), who observed higher overall abundance of mammals in unburnt patches in arid central Australia, but contradicts several other studies that have showed that fire may attract grazing animals into burnt areas because of the initial lush re-growth (Anderson & Müller 2000; Archibald et al. 2005; Sawadogo et al. 2005; Long et al. 2008). We suggest that our data showing ungulate presence 8–10 months post burn may be a more realistic evaluation of the effects of these treatments, rather than an initial short-term movement of ungulates after a burn.

In the sand habitat, both blue wildebeest and zebra increased more post burn in cleared patches compared to uncleared ones, and giraffe increased more post burn in uncleared compared to cleared patches. These results support our second prediction, that is, that we would find a relatively greater post burn increase of grazing species in the cleared compared to uncleared patches, and similarly a greater post burn increase of browsing species in the uncleared patches compared to the cleared ones. Interestingly, kudu declined in all three bush clearing categories post burn, suggesting negative effects of burning regimes on this species, whereas giraffe increased post burn in uncleared and barko cleared patches, and did not decrease in bosvreter cleared patches. We found no consistent results for the mixed feeder impala. These results highlight that fire may cause a decline in available browse, but that giraffe escape such negative effects of fire by foraging at a height level above which fire has an effect on woody vegetation and impala by adopting a mixed feeder strategy.

Finally, our results provided no support for our third prediction (i.e. bush clearing would favor grazers and repel browsers). Instead, bush clearing decreased the occurrence of all ungulate species in the sand habitat, and all species except impala in the red soil habitat. These results are consistent with Ben-Shahar (1992), who demonstrated that impala occurred randomly in cleared and uncleared areas. As a mixed forager, impala make use of various habitats but prefer grass dominated habitat (Wronski 2003). We suggest that impala were attracted to the cleared areas in red soil habitat because of an increased herbaceous cover. Although bush clearing overall had a negative effect on the presence of

ungulate species in the sand and red soil habitat, the method of clearing influenced individual species occurrences. In the sand habitat, giraffe seemed to favor bosvreter-cleared patches slightly more than barko-cleared ones. We found similar results in the red soil habitat for both giraffe and kudu. Since most of the larger trees are unaffected by bosvreter-clearing, these increased occurrences by large obligate browsers could be caused by increased relative food availability on bosvreter-cleared areas.

To conclude, our results suggest that two common restoration options for savannah ecosystems, implementation of prescribed burning to promote habitat heterogeneity and the restitution of bush encroached areas using mechanical removal of woody vegetation, can affect both the overall abundance and the species composition of ungulates, but that these changes do not necessarily follow the predicted trajectories. Although the incomplete sampling design of our study did not allow us to fully resolve the interactive effects of fire and different bush clearing methods across habitats, our results highlight that there are complex ecological consequences of habitat alterations in savannah ecosystems.

Implications for Practice

- Because of the complex and habitat dependent responses that ungulates showed to prescribed burning and mechanical bush clearing, it is difficult to provide general predictions regarding the effects of these anthropogenic alterations of vegetation structure on ungulate space use in savannah ecosystems.
- With the exception of giraffe, burning had a negative effect on ungulate abundance in uncleared patches, but the effect of burning was influenced by bush clearing so that grazers increased post burn in patches, giraffe increased more post burn in uncleared compared to cleared patches, and kudu decreased post burn in both uncleared and cleared patches.
- With the exception of the mixed feeder impala, bush clearing generally had negative effects on ungulate abundance, but the method of bush clearing influenced these effects, particularly for large obligate browsers such as kudu and giraffe.

Acknowledgments

We wish to thank Elias Kalumbwa, Cher Lawrence, Kennedy Leso, Thsidi Maenatja, Pieter Oban, and Boaz Tsebe for assistance with collection of field data. We are grateful to the owners, management, and staff at Lapalala Wilderness for logistic support and permission to conduct the study on the property. John Ludwig and an anonymous reviewer provided constructive comments on the article. Financial support was provided by DST-NRF Centre of Excellence for Invasion Biology, the University of Pretoria research fellowship program and the National Geographic/Waits foundation.

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